

THE GENERIC CLASSIFICATION OF THE AUSTRALIAN TERRESTRIAL ELAPID SNAKES

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The generic arrangement for the Australian elapid snakes has been unstable because, in part, of a lack of phylogenetic data by which monophyletic taxa could be recognised. Recently there have been advances in our understanding of Australian elapid phylogeny. These are summarised and a revised classification is proposed. This is based, as far as the data will allow, on monophyletic units. Evidence for monophyly is drawn from karyotypic, electrophoretic, immunological and internal and external anatomical data. □ *Serpentes, Elapidae, taxonomy, phylogeny, Australia.*

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The Australian terrestrial elapid genera have had an unstable recent taxonomic history. Mengden (1983) thoroughly reviewed the history of Australian elapid snake nomenclature, pointing out the conflicting views of the workers who have tackled this problem, and also noting areas where lack of data inhibited resolution of taxonomic problems. Cogger (1985) also reviewed elapid taxonomy, concluding that its history of largely intuitive analysis of morphological variation was responsible both for the prolonged instability of elapid systematics and the present disagreements over generic boundaries. He anticipated that an objective, biologically well-based taxonomy would only be achieved following a clear understanding of phylogenetic relationships.

For much of the twentieth century snake workers (including Kinghorn [1929; 1956] in his influential guides) followed Boulenger's (1896) arrangement, with relatively few genera diagnosed by features of anal and subcaudal scalation, head shield modification, number of maxillary teeth and general appearance. Worrell (1961; 1963) expressed his conviction that the fauna was more diverse by proposing several new genera, although his views were ignored until McDowell's (1967; 1969a; 1970) studies supported some of Worrell's suggestions. McDowell's comparative anatomical data led him to identify what he called 'natural groups', implying monophyly. Instead, some of his own analysis indicated that he formed some groups based on their *lack* of the derived character state for a feature, so that some, but not all, of his groups are grades, not clades. It is not surprising

therefore, that his different data sets did not always coincide, resulting in a partially inconclusive revision of elapid taxonomy. Cogger (1975 et seq.) adopted a highly subdivided generic arrangement where most diagnosable groups were accorded generic status. Storr (Storr, 1985; Storr et al., 1986), however, has resisted this generic subdivision and has clustered together groups of species which have several external morphological features in common.

Typological thinking has thus led to the definition of diagnosable units (e.g. McDowell's 'natural groups') whose monophyly is assumed but untested. Clearly, as long as genera are defined in this way, classifications will continue to be accepted - or not - on the basis of authority or 'gut feeling', making discussion of the merits or biological validity of competing classifications very difficult.

Recently, data on elapid phylogeny became available in the series of articles forming part of the symposium volume edited by Grigg et al. (1985). These articles presented phylogenetic hypotheses based on karyology and allozyme electrophoresis (Mengden, 1985a; 1985b), immunological comparison of serum proteins (Schwaner, et al. 1985) and soft anatomy (Walach, 1985). None of these studies was complete, in that, for each, certain taxa were unavailable or their relationships were not clearly indicated, and the individual authors were not in a position to benefit from the others' insights. Nevertheless, the different data sets corroborate one another on several points and, more importantly, there are no obvious discordances among the

conclusions arrived at by the different authors. Thus, while a fully resolved, highly corroborated phylogeny for the Australian elapids has not yet been achieved, sufficient data are now available to set up a taxonomic scheme in which the included genera can be defined so as to be monophyletic as well as morphologically cohesive.

For the remainder of this paper I set out the genera which I propose should be recognised, with annotations concerning the evidence for monophyly and the reasons, where appropriate, for the points at which this generic arrangement differs from those accepted by Storr or Cogger. One of the problem areas discussed by Mengden (1983), namely whether 'Elapidae' is the appropriate family name for the Australian proteroglyphs, will not be discussed here. Although biochemical (Mao et al., 1983; Schwaner et al., 1985) and morphological (McDowell, 1967) evidence suggests that the Australian region proteroglyphs (including sea snakes) are monophyletic, suprageneric taxonomy will not be finalised until relationships to exotic proteroglyphs, and other colubroids, are better known. Through this article, 'elapid' is used as a convenient adjective, rather than as a position statement on higher taxonomy.

In arriving at a generic scheme I have used the following guidelines:

1. Genera must be truly monophyletic (holophyletic). Paraphyletic groups have been avoided by making genera either more inclusive or by complete splitting of terminal taxa. Monophyly has been based on the data in Grigg et al. (1985) and on McDowell's data on the derived states of adaptive complexes in venom gland musculature, palatal morphology and hemipenial structure.

2. Apart from the restrictions imposed by (1), genera are composed of species with strong phenetic similarities and ecologies.

3. Where a choice has been possible, genera have been inclusive ('lumped') rather than subdivided ('split') in order to show where species groups have clear sister-groups.

4. Aside from (1)-(3), at least one generic decision (concerning *Notechis*, *Austrelaps*, *Tropidechis*) has been taken (pro tem) to maintain usage of medically significant generic names.

The generic scheme adopted here is summarised in Table 1 and compared to those of Cogger (1986) and Storr (1985; Storr et al.,

1986). For generic synonymies see Cogger et al. (1983).

Acanthophis Daudin, 1803

REMARKS

A chromosomally conservative but morphologically highly derived genus, biochemically well-separated from its nearest relatives, the other viviparous species with entire anal and subcaudal scales.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

antarcticus (Shaw and Nodder, 1802); *praelongus* Ramsay, 1877; *pyrrhus* Boulenger, 1896.

Austrelaps Worrell, 1963

REMARKS

See remarks for *Notechis*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

superbus (Günther, 1858). As presently defined, this is a species-complex (Rawlinson and Hutchinson, in prep.)

Cacophis Günther, 1863

REMARKS

A genus of small cryptozoic snakes associated by most workers with the species here included in *Furina*. Its species retain the primitive *Glyphodon* type of venom gland musculature and (apart from the autapomorphic *squamulosus*) the primitive karyotype. Features which argue for their monophyly with respect to *Furina* are the hemipenis, which is of the derived single type (fide Wallach, 1985) and the characteristic (probably derived) colour pattern of a nuchal pale blotch extending forward over the lores while *Furina* species are possibly monophyletic with respect to *Cacophis* based on their uniformly dark eyes (iris paler than pupil in *Cacophis*). Thus I tentatively support separate recognition of *Cacophis* pending more thorough phylogenetic study.

TABLE 1. Correspondence between generic classification proposed and the generic schemes of Cogger (1985) and Storr (Storr, 1985; Storr et al., 1986).

Cogger	Present Work	Storr
<i>Acanthophis</i>	<i>Acanthophis</i>	<i>Acanthophis</i>
<i>Austrelaps</i>	<i>Austrelaps</i>	
<i>Drysdalia</i>	<i>Drysdalia</i> ← part	<i>Notechis</i>
<i>Echiopsis</i>	<i>Echiopsis</i> ← part	
<i>Elapognathus</i>	<i>Elapognathus</i> ← part	
<i>Notechis</i>	<i>Notechis</i>	
<i>Demansia</i>	<i>Demansia</i>	<i>Demansia</i>
<i>Cacophis</i>	<i>Cacophis</i>	<i>Cacophis</i>
<i>Furina</i>	<i>Furina</i>	<i>Furina</i>
<i>Glyphodon</i>		
<i>Hemiaspis</i>	<i>Hemiaspis</i>	<i>Hemiaspis</i>
<i>Hoplocephalus</i>	<i>Hoplocephalus</i>	<i>Hoplocephalus</i>
<i>Denisonia</i>	<i>Denisonia</i> ← part	<i>Denisonia</i>
<i>Suta</i>	<i>Suta</i> ← part	
<i>Unechis</i>	<i>Suta</i> ← part	
<i>Rhinoplocephalus</i>	<i>Rhinoplocephalus</i>	<i>Rhinoplocephalus</i>
<i>Cryptophis</i>		<i>Cryptophis</i>
<i>Oxyuranus</i>	<i>Oxyuranus</i>	<i>Oxyuranus</i>
<i>Parademansia</i>		
<i>Pseudechis</i>	<i>Pseudechis</i>	<i>Pseudechis</i>
<i>Pseudonaja</i>	<i>Pseudonaja</i>	<i>Pseudonaja</i>
<i>Tropidechis</i>	<i>Tropidechis</i>	<i>Tropidechis</i>
<i>Neelaps</i>		
<i>Simoselaps</i>	<i>Simoselaps</i> ← part	
<i>Vermicella</i>	<i>Vermicella</i>	<i>Vermicella</i>

DIAGNOSIS
See Cogger (1986).

(Günther, 1862); *vestigiata* (de Vis, 1884) (from Storr et al., 1986; Ingram, 1990; and pers. obs.).

INCLUDED SPECIES
harriettae Krefft, 1869; *krefftii* Günther, 1863; *squamulosus* (Duméril, Bibron and Duméril, 1854).

Denisonia Krefft, 1869

Demansia Günther, 1858

REMARKS
It is clear from all of the studies in Grigg et al. (1985) that this genus, even in the restricted sense of Cogger (1986), is polyphyletic. The type (*maculata*) and *devisi* are sister species, but more closely related to *Drysdalia* than to the other species retained in *Denisonia* by Cogger (*fasciata* and *punctata*) or the species placed by Storr in his expanded *Denisonia*. The pronounced difference in morphology and ecology between the two species retained here in *Denisonia* and their nearest relatives, *Drysdalia* (nocturnal, broad head-and-body species with glossy scales, elliptical pupils, versus diurnal, gracile species with matt scales and round pupils) argues for separate generic status for these two groups.

REMARKS
A chromosomally unique genus whose members have a derived morphology (convergent on Holarctic racers) for highly active diurnal foraging. Biochemical evidence indicates wide divergence from its nearest relatives (*Pseudechis* and *Pseudonaja*).

DIAGNOSIS
See Cogger (1986).

INCLUDED SPECIES
calodera Storr, 1978; *olivacea* (Gray, 1842); *papuensis* (Macleay, 1877); *psammophis* (Schlegel, 1837); *reticulata* (Gray, 1842); *rufescens* Storr, 1978; *simplex* Storr, 1978; *torquata*

AMENDED DIAGNOSIS
As in Cogger (1985) with the following additions: Pupil vertically elliptic, iris of eye pale.

Distinguished from some superficially similar species of *Suta* by venom gland musculature of the *Oxyuranus* type (versus the *Psenedechis* type), retention of the deeply forked hemipenis (simple in *Suta*), diploid number of 34 with pair 5 sex chromosomes (versus 30 with pair 4 sex chromosomes) and upper labials strongly barred with white and dark brown.

INCLUDED SPECIES

devisi Waite and Longman, 1920; *maculata* (Steindachner, 1867).

Drysdalia Worrell, 1961

REMARKS

The distinctive pair 5 (rather than pair 4) sex chromosomes (shared with *Denisonia* s.s.) separate this morphologically cohesive group of small diurnal skink predators from *Notechis* and its relatives. *D. coronata*, which lacks the chromosomal synapomorphy, is nevertheless close to the other three species based on anatomical features (Wallach, 1985). On biochemical evidence (Schwaner et al., 1985; Mengden, 1985a) these snakes are less closely related to *Notechis* than are several morphologically divergent genera, notably *Hoplocephalus* and *Tropidechis*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

coronata (Schlegel, 1837); *coronoides* (Günther, 1858); *mastersii* (Krefft, 1866); *rhodogaster* (Jan, 1873).

Echiopsis Fitzinger, 1843

REMARKS

Undoubtedly a close relative of *Notechis* on the basis of strong internal anatomical (Wallach, 1985) and biochemical similarities (Schwaner et al., 1985; Mengden, 1985b), as well as the phenetic similarities noted by Storr (1982). However, its derived *Acanthophis*-like habitus, including the subdivided temporal scalation noted by Mengden (1985a) and vertically elliptical pupil, and the absence of the derived *Notechis* karyotype, support separate generic status for at least *curta*. Mengden (1985a) also reported that *curta* showed venom properties with *Acanthophis*, adding to the list of features suggesting a possible sister-group relationship

between these two taxa, rather than between *curta* and *Notechis scutatus*. *Brachyaspis atriceps* Storr, 1980, has not been studied and may, as Storr suggests, be closer to his *Denisonia* (*Suta* in my sense) than to *curta*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

curta (Schlegel, 1837).

Elapognathus Boulenger, 1896

REMARKS

The general relationships of this monotypic genus clearly lie with the large group of viviparous species having entire anal and subcaudal scales. Storr (1982) partly expressed this in synonymising *Elapognathus* with *Notechis*. However, the precise sister species of *E. minor* is not identified by the available data. It retains the primitive $2n = 36$ karyotype and is biochemically rather divergent from its relatives. Wallach's analysis fails to consistently identify a sister taxon. In 'gestalt', *E. minor* is most similar to juvenile copperheads (esp. *superbus*, s.s.) and Storr placed it in his *Notechis* on the basis of shared similarities with *scutatus*, *superbus* and *Drysdalia*. Storr dismissed the single generic character (no post-fang maxillary teeth) by making a general statement about the cautious use of dental characters in snakes. Nevertheless, his taxonomic characters for *Notechis* (s.l.) define a paraphyletic taxon (*Tropidechis*, *Hoplocephalus*, *Denisonia* s.s., and possibly even *Acanthophis*, should all be included) so that his data have defined only a grade of organisation (the primitive morphology for this group of genera?) rather than a strictly monophyletic taxon. My conclusion is that *Elapognathus* is, like *Echiopsis*, morphologically distinct (fang only on the maxilla, a derived character state) and lacks the apomorphic chromosomal feature of either *Notechis* or *Drysdalia*. Its single species, *E. minor*, is, on the basis of biochemical data, a very distinct species with no obvious sister taxon, and I favour its recognition.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

minor (Günther, 1863)

Furina Duméril, 1853

REMARKS

Furina and *Glyphodon* are similar small snakes characterised by divided anal and subcaudal scales, a cryptozoic way of life and, in most species, white to red nuchal patches. This pair has been least studied chromosomally and biochemically, so that there is rather little well-constructed phylogenetic data available. The genera are separated by features (presence/absence of a divided nasal) of unknown phylogenetic significance. In Wallach's analysis, the species included in the two genera tend to fall out as each-other's closest relatives, but do not form sub-groups matching the current generic boundaries; indeed, with every alteration in algorithm, the branching order changes. Mengden, on the basis of unspecified data, groups the pair as a monophyletic cluster of early divergence, with *Cacophis* the sister group of *Furina* (*diadema* only) plus *Glyphodon* (including *F. ornata*). The boundary between *Furina* and *Glyphodon* seems tenuous, especially the intermediacy of *F. ornata* with respect to *F. diadema* (generotype) on one hand and *G. tristis* (generotype) on the other. This lineage needs more study, pending which I feel there is insufficient data of phylogenetic significance by which the two genera can be justified. Uniting them under the oldest available name does, with seeming reliability, give rise to a monophyletic unit, which is moreover, relatively cohesive in ecology.

DIAGNOSIS

A genus of glossy-scaled (15-21 rows at mid-body), snakes with a divided anal and divided subcaudals. Often (not *F. barnardi* or *F. dunmalli*) with a pale (white to red) nuchal blotch. Five or more teeth on each maxilla behind the fang. Head somewhat to markedly wider than neck and lacking a canthus rostralis.

INCLUDED SPECIES

barnardi (Kinghorn, 1929); *diadema* (Schlegel, 1837); *dunmalli* (Worrell, 1955); *ornata* (Gray, 1842); *tristis* (Günther, 1858).

Hemiaspis Fitzinger, 1860

REMARKS

A karyotypically unique pair of species, showing the unusual combination of divided anal, entire subcaudals and viviparity. Electrophoretic (? and chromosomal) data of Mengden sug-

gested a very close relationship between the two species, as did Wallach's morphological data. The sister group of these two is not well established, but it seems a well-defined taxon.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

damelii (Günther, 1876); *signata* (Jan, 1859).

Hoplocephalus Wagler, 1830

REMARKS

Another chromosomally unique and morphologically well-defined genus, whose members possess the arboreal adaptation of angular ventrals and have markedly broad heads distinct from the narrow neck. Very closely related, an immunological (Schwaner et al., 1985) and morphological (Wallach, 1985) data to *Notechis* and *Tropidechis*. The phylogenetic position of this genus gives one of the strongest indications that Storr's concept of *Notechis* is paraphyletic, implying that his generic diagnosis is based at least in part on symplesiomorphies.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

bitorquatus (Jan, 1859); *bungaroides* (Schlegel, 1837); *stephensii* Krefft, 1869.

Notechis Boulenger, 1896

REMARKS

At present a controversial genus containing either two or a single species (Cogger, 1986; Schwaner pers. comm.), or a cluster of species which are surface-dwelling, viviparous, have entire anal and subcaudal scales and are otherwise morphologically conservative (Storr, 1982). Immunological, chromosomal and morphological studies all indicate that Storr's concept is paraphyletic.*

*And nomenclaturally invalid. Storr (1982) dismissed *Echiopsis* Fitzinger as a nomen oblitum although declaration of a name as 'forgotten' could no longer be made after 1 January 1973. Fitzinger's (1843) names are widely regarded as available and are in wide use (including *Echiopsis*, see Cogger et al., 1983). Thus the correct name for Storr's genus should have been *Echiopsis* Fitzinger, 1843, not *Notechis* Boulenger, 1896.

However, there is a strong indication that *scutatus* is very closely related to the *Austrelaps superbus* complex, the two sharing (with *Tropidechis*) a uniquely derived karyotype and being very similar biochemically, anatomically and ecologically. Accordingly, I would favour the elimination of *Austrelaps* and the transferral of the *superbus* complex to *Notechis*. However, the precise relationships of *scutatus*, the *superbus* complex and *Tropidechis carinatus* are not yet established. The three taxa differ in minor features of proportions and scalation and are, based on the chromosomal synapomorphy, each other's closest relatives. Amalgamation of the three would be a simple answer, except for the nomenclatural problem of the synonymisation of *Notechis* under the older *Tropidechis*. Because of the widespread use of the junior name, phylogenetic data would need to be compelling before such a destabilising revision of the existing taxonomy would be justified - in fact it could well lead to appeals to the ICZN to suppress *Tropidechis* in favour of *Notechis*. Pending detailed phylogenetic knowledge, *Tropidechis* and *Notechis*, and therefore *Austrelaps* should remain separate genera, although the close relationship between them should be borne in mind. *Tropidechis* is derived with respect to *Notechis* (s.s.) in its keeled scalation and increased midbody scale count, while *Austrelaps* differs in its derived *Pseudechis* type (rather than *Oxyuranus* type) of venom gland musculature.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

scutatus (Peters, 1861).

Oxyuranus Kinghorn, 1923

REMARKS

Covacevich et al. (1981) set out a range of characteristics which argued for sister-species relationship and congeneric status of *Pseudechis scutellatus* Peters, 1868 and *Diemenia microlepidota* McCoy, 1879. Cogger preferred to continue recognition of a monotypic *Parademansia* for *microlepidota*, but the additional data from the 1985 symposium reinforce the close relationship of these two species and further argue for their inclusion in a single genus.

DIAGNOSIS

See Covacevich et al. (1981).

INCLUDED SPECIES

microlepidotus (McCoy, 1879); *scutellatus* (Peters, 1868).

Pseudechis Wagler, 1830

REMARKS

A morphologically cohesive group retaining a primitive karyotype, but closely-related on the basis of immunological data (Schwaner et al., 1985) and monophyletic based on morphology (Wallach, 1985) and allozyme comparisons (Mengden et al., 1986).

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

australis (Gray, 1842); *butleri* Smith, 1982; *colletti* Boulenger, 1902; *guttaus* de Vis, 1905; *papuanus* Peters and Doria, 1878; *porphyriacus* (Shaw, 1794).

Pseudonaja Günther, 1858

REMARKS

Another well defined and monophyletic genus, although its alpha taxonomy is presently very unsatisfactory. Wallach's (1985) contention that *modesta* was not allied to the other species in this genus was refuted on several ground by Mengden (1985b).

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

affinis Günther, 1872; *guttata* (Parker, 1926); *ingrami* (Boulenger, 1908); *modesta* (Günther, 1872); *nuchalis* Günther, 1858; *textilis* (Duméril, Bibron and Duméril, 1854).

Rhinoplocephalus Müller, 1885

REMARKS

Another genus treated discordantly by Cogger and Storr. Long regarded as a monotypic genus (on the strength of the fused internasals and nasals) Storr greatly expanded the genus to include the other small, pale-bellied and dark-eyed semi-fossorial/nocturnal species placed by Cogger in *Unechis*. Mengden's and Wallach's studies partially support Storr, in that they indicate that some other species are closely related

to *bicolor*, the type of *Rhinoplocephalus*, these being the two species of *Cryptophis* plus the type species of *Unechis*, *U. boschmai* (formerly *U. carpentariae*) and possibly *U. nigrostriatus*. However, the other small black-headed snakes (the *gouldii* complex) show a closer relationship to *Suta* and 'Denisonia' *punctata* and 'D.' *fasciata* than they do to *bicolor*. Thus I favour expanding *Rhinoplocephalus* to include the four close relatives mentioned above (including the types of *Cryptophis* and *Unechis*), but transferring the remaining species of Storr's *Rhinoplocephalus* to *Suta* (see below).

REVISED DIAGNOSIS

A group of small to moderate-sized species lacking contrasting dark head colouring (apart from *R. nigrostriatus*), with glossy midbody scales in 15 rows, anal and subcaudals entire, eye small with black iris, indistinguishable from pupil. Head, slightly to moderately depressed, no canthus. Distinguished externally from some superficially similar species of *Suta* by deeper, blunter head, absence of contrasting colour pattern (except black-headed *R. nigrostriatus*) and/or longer tails (subcaudal counts exceed 40 in most species [not *boschmai*], versus 40 or fewer in most *Suta*). Further distinguished from other genera by the unique karyotypes (not present in *bicolor*), $2n = 36$ (20 M, 16 M) or 40.

INCLUDED SPECIES

bicolor Müller, 1885; *boschmai* (Brongersma and Knaap-Van Meeuwen, 1961); *nigrescens* (Günther, 1862); *nigrostriatus* (Krefft, 1864); *pullidiceps* (Günther, 1858).

Simoselaps Jan, 1859

REMARKS

Storr and Cogger both noted that the small, mostly cross-banded fossorial snakes of arid Australia fall into several distinct subgroups, based on body, head and head-shield proportions which reflect ecological specialisation (Shine, 1984). Cogger separated some of these as distinct genera, but Storr united all in *Vermicella*, while identifying subgeneric groups having similar morphologies. Karyotypic data show that at least two of Cogger's genera (*Neelaps* and *Vermicella* s.s.) retain the primitive karyotype, while the types of two other genera or sub-genera (*Simoselaps* and *Brachyuropis*) have derived karyotypes. Of the latter pair, Mengden (1985a) derived the karyotype of (*Brachyuropis*) *semi-*

fasciatus from that of (*Simoselaps*) *bertholdi*, implying a phylogenetic relationship between these taxa. Wallach's (1985) analysis shows all of the burrowing group consistently forming a monophyletic lineage, but the branching order within the group is not unequivocal. Only *Cacophis warro* de Vis, 1884, fails to fall out with the other burrowers, but Mengden's report of its showing the uniquely derived karyotype of *bertholdi* would argue for retention in the same genus as this species at least. No authors seem to have taken account of McDowell's (1969a) report of the distinctive biting apparatus present in all but *annulata* (and presumably *multifasciata*). This functional complex argues strongly for monophyly of at least all of the species except the type of *Vermicella*. *Furina annulata* Gray, 1841 is a remarkably primitive species, retaining the plesiomorphic state of the karyotype, venom gland musculature, hemipenis and palatine bone. As the true bandy-bandy (*Vermicella* s.s.) show none of the synapomorphies which unite some or all of the remaining species, there are no strong grounds, as McDowell (1969a) pointed out, for placing *annulata* with the other burrowers grouped together here as an expanded *Simoselaps*. Although morphological subgroups certainly exist within *Simoselaps*, relationships among them are obscure, and I prefer to recognise the probable monophyly of this group rather than itemising variation of uncertain phylogenetic significance.

DIAGNOSIS

A group of small (less than 0.6 m total length), glossy scaled semi-fossorial snakes with anal divided, short tails with 35 or fewer paired subcaudals and showing variation in snout shape and body proportions analogous to those seen in *Ramphotyphlops*. Rostral always projecting but varying in profile from bulbous (e.g. *bimaculatus*) to wedge-shaped (e.g. *fasciolatus*) to upturned and angular (e.g. *semifasciatus*). No canthus rostralis. Body short and dumpy to elongate, but ventrals fewer than 230. Dark parietal and nuchal blotches always present, body usually yellow, orange or reddish, generally with darker reticulated or cross-banded pattern.

INCLUDED SPECIES

anomala (Sternfeld, 1919); *approximans* (Glauert, 1954); *australis* (Krefft, 1864); *bertholdi* (Jan, 1859); *bimaculata* (Duméril, Bibron and Duméril, 1854); *calonota* (Duméril, Bibron and Duméril, 1854); *fasciolatus* (Günther,

1872); *incincta* Storr, 1968; *littoralis* Storr, 1968; *minima* (Worrell, 1960); *roperi* (Kinghorn, 1931); *semifasciatus* (Günther, 1863); *warro* (de Vis, 1884).

Suta Worrell, 1961

REMARKS

Preceding discussion on *Denisonia* and *Rhinoplocephalus* has alluded to the fact that several species share a close relationship with the type species of *Suta* (*Hoplocephalus sutus* Peters, 1863). The most compelling evidence is the uniquely shared $2n = 30$ karyomorph, present in *Suta*, 'Denisonia' *fasciata* and 'D.' *punctata*, and the 'Unechis' *gouldii* species group. All are morphologically similar in being, like *Rhinoplocephalus*, small, glossy scaled cryptozoic species with entire anal and subcaudal scales. All species tested by Schwaner et al. (1985) also proved to be close to the *Notechis* group, and all of these species fall out as each other's closest relatives in Wallach's analysis. All have the derived *Pseudechis* type of venom gland musculature (McDowell, 1970). Storr et al. (1986) separated the three species with pale iris colour (*suta*, *ordensis* and *fasciata*) from the remainder, and place them with superficially similar species in his *Denisonia*. However, the pale iris is evidently a retained primitive feature, and eye colour is known to be intraspecifically variable in *ordensis* (Storr et al., 1986, p. 75).

REVISED DIAGNOSIS

A group of small to moderate-sized snakes with a consistent colour pattern of dark head markings (often a black to brown cap) and lighter brown body (cross-banded in *fasciata*), midbody scales very glossy, in 15-21 rows, anal and subcaudal scales entire. Head slightly to markedly depressed; no canthus rostralis. Eye uniformly black in most species, but paler than pupil, which contracts to a vertical ellipse, in *suta*, *fasciata* and most *ordensis*. Further distinguished by unique $2n = 30$ karyomorph. (See also *Rhinoplocephalus*.)

INCLUDED SPECIES

dwyeri (Worrell, 1956); *fasciata* (Rosén, 1905); *flagellum* (McCoy, 1878); *gouldii* (Gray, 1841); *monachus* (Storr, 1964), *nigriceps* (Günther, 1863); *ordensis* (Storr, 1984); *punctata* (Boulenger, 1896); *spectabilis* (Kreffft, 1869); *suta* (Peters, 1863). Probably

Brachyaspis atriceps Storr, 1980, belongs here as well.

Tropidechis Günther, 1863

REMARKS

See remarks for *Notechis*.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

carinatus (Kreffft, 1863).

Vermicella Günther, 1858

REMARKS

See remarks for *Simoselaps*. Aside from the unique colour pattern of black and white bands, the two species of *Vermicella* share a very to extremely attenuate body. Ventral counts in *V. annulata* range as high as 243 (Storr et al., 1986) (250 or fewer, generally less than 200, in other Australian elapid taxa) while in *V. multifasciata* counts range up to 290 (Cogger, 1986). Western populations of this genus have been described as a subspecies, *snelli* Storr, 1968, which Cogger (1986) placed with *annulata* but Storr et al. (1986) placed with *multifasciata*. The very high ventral count of *snelli* (to 318; Storr et al., 1986) indicates a closer relationship to *multifasciata*, although it lacks the latter's derived fusion of internasal and prefrontal shields.

DIAGNOSIS

See Cogger (1986).

INCLUDED SPECIES

annulata (Gray, 1841); *multifasciata* (Longman, 1915).

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